

## An ecological comparison between standard and chromosomally divergent House mice in Northern Scotland

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### Abstract

In western Europe there are populations of the house mouse that diverge in karyotype from the standard 40-chromosome complement as a result of Robertsonian fusions between pairs of chromosomes. Very little is known about the ecology of such Robertsonian populations of the house mouse. The present study focuses on the Robertsonian system of north east Scotland. We distinguish seven "chromosomal zones" along north-south and east-west transects ( $2n = 32$  in the extreme north east,  $2n = 34$  S(outh),  $2n = 34$  W(est),  $2n = 36$  S,  $2n = 36$  W,  $2n = 40$  S,  $2n = 40$  W). We describe and compare the different chromosomal zones in relation to their habitat and population characteristics. The  $2n = 32$  chromosomal race is characterised by the lowest density as well as the lowest frequency of pregnant and lactating females. The highest densities are found in both the  $2n = 40$  zones. Intermediate chromosomal zones appear to be separated from each other by habitat where the house mouse does not occur. Thus, passive transport may represent the only means by which mice could move between zones. Within the 32, 34 and 36 S zones movements of materials occur, while farmers from these areas have few, if any, interactions with farmers in the other zones. This pattern of agricultural contact would tend to facilitate chromosomal flow between the 32, 34 and 36 S chromosomal zones and isolate them from the three other zones. Chromosomal flow between the 32 zone and adjacent areas may threaten the low-density, low-fertility 32-chromosome race with extinction.

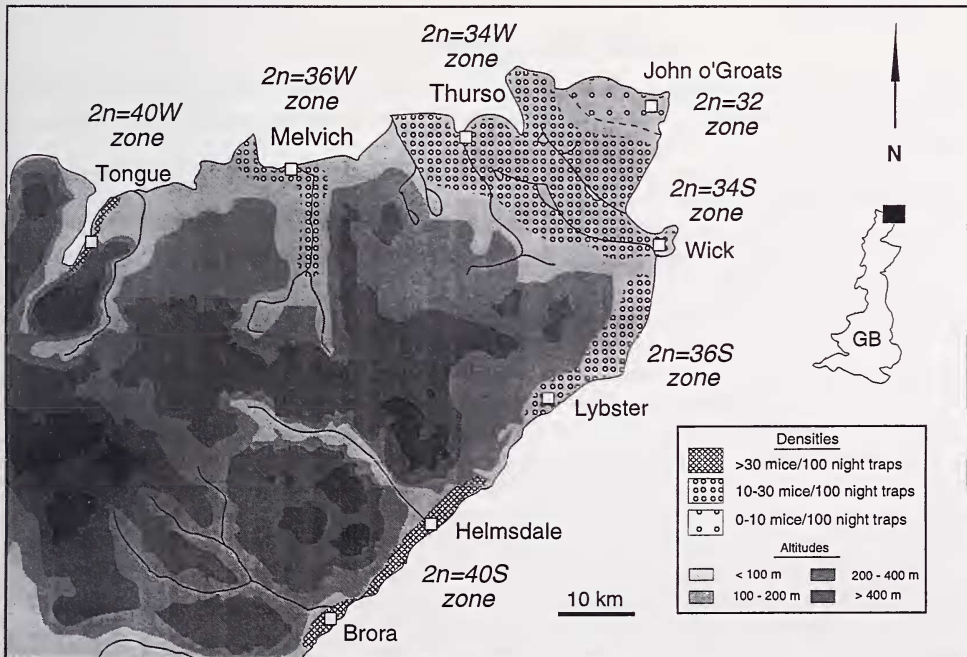
### Introduction

Several populations of the house mouse (*Mus musculus domesticus*) diverge chromosomally from the standard type ( $2n = 40$  chromosomes, all with terminal centromeres), through the fusion of pairs of chromosomes at their centromeres (Robertsonian fusions). These mutations have been found in natural populations of mice and involve most autosomes. Robertsonian populations occur in Europe and northern Africa (BAUCHAU 1990), and based on archaeozoological and molecular data, it is largely accepted that this divergence took place less than 10,000 years ago (AUFFRAY et al. 1990 b, NACHMAN et al. 1994).

Very little is known about the ecology of Robertsonian populations of the house-mouse (AUFFRAY et al. 1990 a, GANEM 1991, 1993; SAID and BRITTON-DAVIDIAN 1991; BERRY et al. 1992; HAUFFE 1993). This is due to the fact that most studies concerning these populations have been aimed solely at a description of karyotypes. However, estimates of population size, rates of turnover and extinction, and patterns of social and geographical structure of nearby Robertsonian and standard populations could help to: a) understand past events which promoted the fixation of Robertsonian fusions and their subsequent spread (assuming that we can relate present-day ecology to past ecology), b) analyse present dynamics of hybrid zones between standard and Robertsonian populations, and c) make predictions about future spread or extinction of such populations.

This study focuses on Robertsonian populations occurring in the extreme north of mainland Scotland, where there is a race characterised by 32 chromosomes (homozygous for 4 centric fusions: 4.10, 9.12, 6.13, 11.14; SCRIVEN and BROOKER 1990; SEARLE 1991), which forms a hybrid zone with the more widespread standard type. The hybrid zone extends along both the northern and eastern coast of the counties of Caithness and Sutherland. It has a staggered structure, such that there is a  $2n = 36$  race (homozygote for two centric fusions: 4.10, 9.12) in the middle of the hybrid zone (SEARLE et al. 1993). This staggered structure allow to distinguish different "chromosomal zones" corresponding to zones where a particular diploid number predominate. This situation provides a particularly interesting model to address the above considerations.

For the ecological study presented here we sampled seven "chromosomal zones" (Fig. 1), the  $2n = 32$  zone in the vicinity of John o'Groats, areas immediately south and west of this zone where mice had karyotypes close to  $2n = 34$  (34S and 34W respectively), and even more southerly and westerly zones characterised by  $2n = 36$  and  $2n = 40$  (36S, 36W, 40S, 40W). This study will address the following questions, i) do the chromosomal zones present different habitat characteristics, related or not to agricultural practices? ii) are there differences in fertility between Standard and Robertsonian populations? iii) are habitat and population characteristics relevant to the chromosomal evolution of house mice in northern Scotland?



**Fig. 1.** Geographic location of the different chromosomal zones described in this study with special reference to the densities of mice in these zones. The area shown constitutes the counties of Caithness (to the north-east) and Sutherland (to the south-west) with the boundary occurring in a line approximately between Melvich and Helmsdale.

## Material and methods

Forty one different farms were visited during two field sessions (March, 1992; September, 1992), as well as three outdoor localities (completely independent of human activities). In March 1992, mice were found in 18 out of 26 farms sampled. In September 1992 out of 24 farms, 16 produced mice. Six farms were successfully sampled during both trapping sessions, these will allow to detect seasonal differences. A total of 280 mice were trapped during 1900 trapnights (Tab. 1). Despite extensive trapping in the outdoor localities (300 trapnights) no house mice were trapped while wood mice (*Apodemus sylvaticus*) were numerous in one of the sites and common shrews (*Sorex araneus*) were present in another.

Longworth traps were baited with peanut butter and were set in several contiguous and non-contiguous rooms in each farm; the number of traps set depended on room sizes and varied between 2 to 20; the trapping period varied between 3 to 7 nights depending on trapping success. Trapping sites were noted precisely for each mouse, and when the same or very close traps (less than 1 metre apart) repeatedly caught mice, this was recorded as evidence of spatial association of mice.

From the data collected, population sizes for each farm are expressed as number of mice/100 trap nights, and sex ratio is described in terms of total number of males/total number of females. Trapping visits which resulted in nil returns were excluded from the analysis.

For each chromosomal zone the mean body weight of mice caught, and the frequency distribution of body weights were also analysed.

The reproductive condition of mice was assessed in live individuals in the field. For live individuals we calculated the ratio of the number of pregnant and lactating females/total number of females, and the ratio of number of males with descended testes/total number of males. Testis and seminal vesicle weights were measured on post-mortem specimens (Mettler AE 163 balance) which were sacrificed after being kept for 3 months in male-female pairs under laboratory conditions.

## Results

### Habitat characteristics (Tab. 1, Fig. 1)

Many small and some medium sized farms occur in the 32 zone. They are bordered by the sea, agricultural fields or heather moorland. Most of the farms do not have large stocks of grain and straw.

The 34S zone is separated from the 32 zone by hilly ground covered in heather moorland and peat bogs, where many wood mice occur (outdoor site n° 1). The 34S zone is connected to the 34 W zone by a series of small and large farms.

The 34 W zone is separated from the 32 zone by large sand dunes. Some medium and large farms in the 34 W zone show intensive agricultural activity, very favourable for mice, and could constitute a mouse reservoir for the zone.

The 36 W and 36 S zones are separated from each other by geographical features such as hills, lochs, and woods, in which there are few farms. The 36 S zone extends from Wick to Lybster, but is limited to a strip of land along the east coast. It is characterised by a series of closely-located active small farms surrounded by cultivated fields.

The 36 W zone occurs south west of Thurso, and south of Melvich Bay. It is limited to several small and medium sized farms occurring along the Halladale river. This agricultural strip is surrounded by natural landscape, mostly uninhabited by humans. It is separated from the 34 W zone by natural geographical features.

The 40 W and 40 S zones are approximately 75 km distant from each other, and coincide with the western and southern borders of Caithness. They are isolated from the closest 36 zones by hills and mountains where farms are rare. They mainly consist of large to very large farms, which contain abundant resources for mice. The 40 W zone seems to be mainly limited to the area of Tongue which is surrounded by the sea, mountains and loch, uninhabited zones where farms are rare.

In the different zones farmers tend to regulate mice by the use of cats; poison is not used extensively.

**Table 1.** Description of localities where mice were caught  
 Sampling session 1: March 1992. Sampling session 2: September 1992

L: large sized farm, > 400 m<sup>2</sup>

M: medium sized farm, 200 < x < 400 m<sup>2</sup>

S: small sized farm, < 200 m<sup>2</sup>

Chromosomal zone	Farm grid reference (Ordinance Survey)	Sampling session	Number of mice	Size	Presence of predators (cat, dog). Use of poison	Presence of other small mammals
32	3388/9709 (Biel of Duncasby)	/2	/1	M	cat	<i>Apodemus sylvaticus</i>
	3378/9732 (John o' Groats 5)	1/2	4/2	M	cat	<i>Apodemus sylvaticus</i>
	3376/9719 (John o' Groats 6)	/2	/2	S	cat	/
	3372/9734 (Mill)	/2	/1	S	/	/
	3368/9734 (John o' Groats 7)	/2	/1	S	cat	/
	3360/9736 (Pier)	/2	/6	S	/	/
	3355/9724 (Canisbay)	/2	/4	S	/	<i>Apodemus sylvaticus</i> , <i>Microtus agrestis</i>
	3354/9729 (Seater)	1/2	10/4	L	/	<i>Microtus agrestis</i>
	3341/9729 (Kirkstyle)	1/2	12/0	S	dog	<i>Sorex araneus</i>
34 S	3357/9627 (Keiss 1)	1/	5/	S	cat	<i>Apodemus sylvaticus</i>
	3327/9512 (Haster)	/2	/1	S	cat	/
36 S	3344/9447 (Thrumster)	1/	9/	S	poison/cat	/
	3346/9437 (Sarlet)	1/	5/	S	cat	/
	3235/9380 (Smerlie 1)	1/2	13/13	S	/	/
	3238/9379 (Smerlie 2)	1/2	4/6	S	cat	/
	3239/9379 (Smerlie 3)	1/2	8/7	S	poison	<i>Sorex araneus</i>
40 S	3070/9201 (Ousdale)	1/2	8/0	L	cat	/
	2957/9107 (Crakaig)	1/2	23/0	L	poison	when 0 mice <i>Apodemus sylvaticus</i> ; <i>Sorex araneus</i>

Table 1. (Continued)

	2925/9078 (Brora 1)	1/2	10/26	L	cat	/
	2919/9078 (Brora 2)	/2	/19	S	dog	<i>Apodemus sylvaticus</i>
34 W	3234/9734 (Brough)	/2	/15	M	cat	/
	3211/9713 (Dunnet 2)	/2	/1	S	cat	/
36 W	2895/9521 (Bunahoun)	1/	8/	S	dog, cat	<i>Microtus agrestis</i>
	2894/9582 (Achiemore)	1/	9/	M	/	/
	2889/9574 (Upper Bighouse)	1/	7/	S	cat	<i>Apodemus sylvaticus</i>
	2888/9566 (Laidham)	1/	2/	M	cat	/
40 W	2584/9539 (Ribigill)	1/	35/	L	poison	/

### Population characteristics

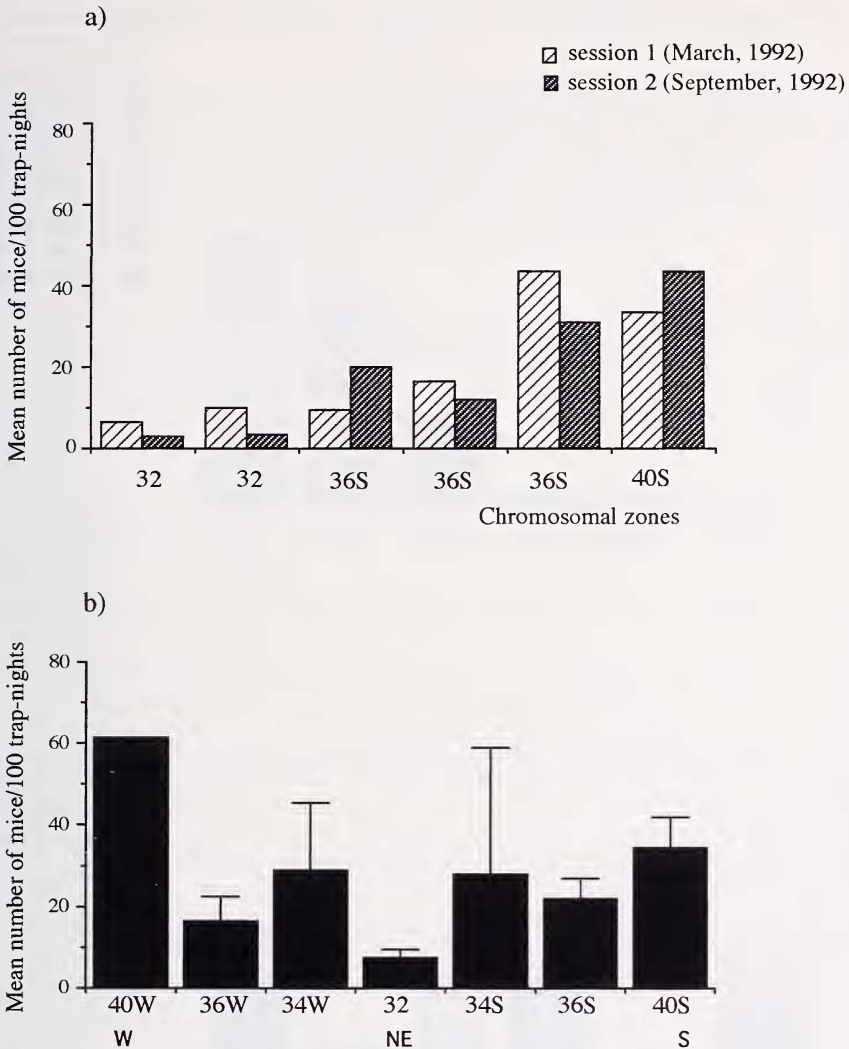
Six farms from the three main zones of the north-south transect (32, 36 S, 40 S) were successfully sampled during both trapping sessions. The analysis shows that densities within each farm, and thus within each zone, did not differ between sessions (Kruskal-Wallis test,  $KW = 0.4$ ,  $p = 0.5$ ), however, densities were different between zones ( $KW = 9.4$ ,  $p = 0.009$ ; Fig. 2 a).

The same difference between zones was observed when the entire set of data was analysed ( $KW = 12.75$ ,  $p = 0.05$ ; Fig. 2 b). The Robertsonian 32 zone is characterised by the lowest density of mice, and the 40 S and 40 W zones by the highest densities.

Sex-ratios were not significantly different between zones. The average sex-ratio was  $1.2 \pm 0.2$ ; this does not differ significantly from 1.0. Only in the 32 zone males showed a tendency to be more numerous than females during both sessions (respectively 69.2 and 62.0% of males).

Taking all the different sampled farms, we found that various numbers (2–8) and combinations of mice (males, females or males and females, in different proportions of adults, more than 16 g, and immatures, less than 14 g) may occur in close spatial proximity.

The weight structure of populations was assessed by subdividing mice into six categories (< 10 g, 10–12 g, 12–14 g, 14–16 g, 16–18 g, > 18 g). Males and females showed similar distributions and there were no significant differences between chromosomal zones or between trapping sessions (Kolmogorov-Smirnov two samples tests  $p > 0.05$ ). However, two patterns of weight frequency distribution occur (Fig. 3). One is the "adult dominant" type (Fig. 3 a) found during both trapping sessions in the 36 S zone, and during the first session in the 40 S, 32 and 40 W zones. The alternative "all age classes" type (Fig. 3 b) characterised the 40 S and 32 zones during the second session, and the 36 W zone during the first session.

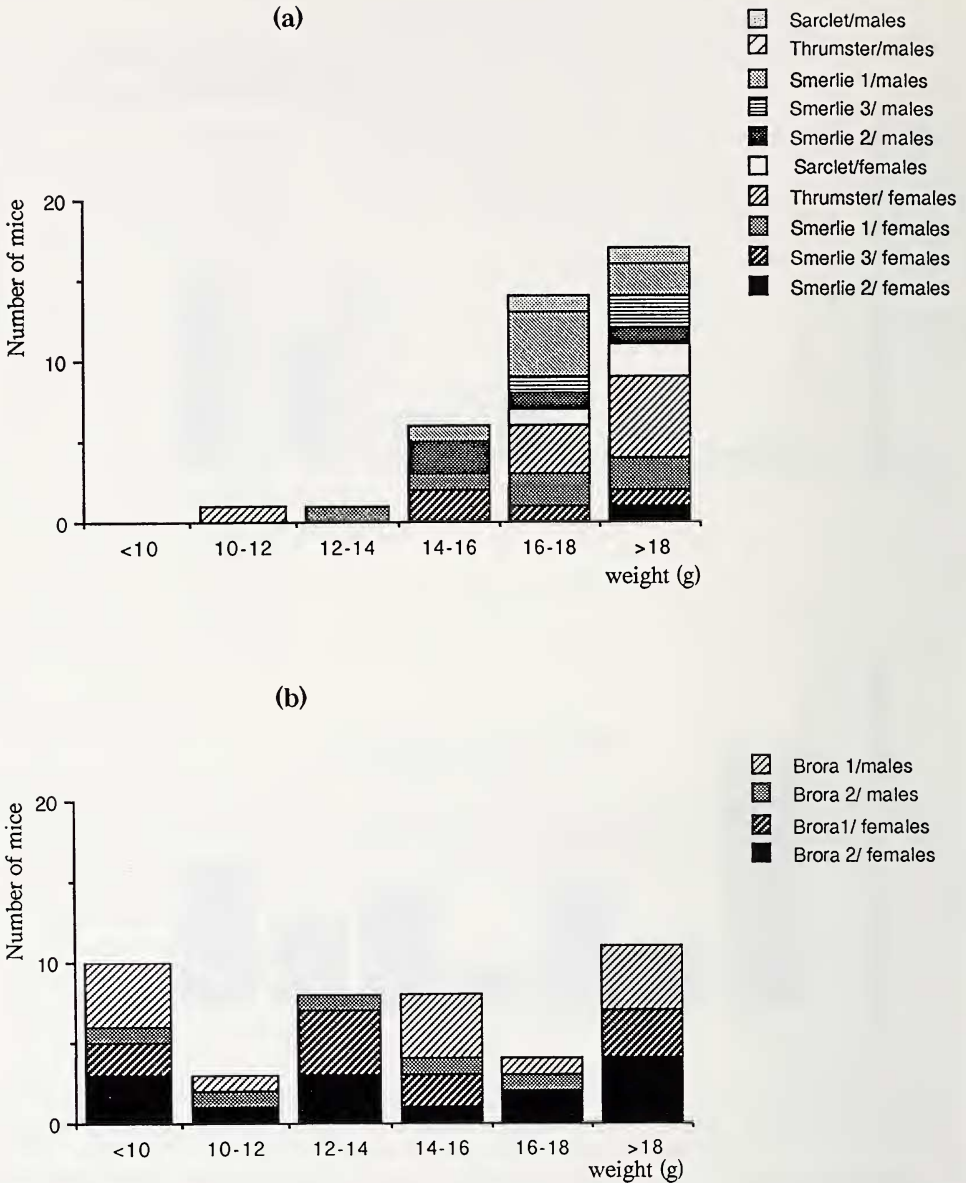


**Fig. 2.** a) Variation in number of mice (mean  $\pm$  S.E.) at six different farms along a 80 km north-south transect through the Scottish hybrid zone sampled during both trapping sessions. (Farms from left to right: John o'Groats 5, Seater, Smerlie 1, 2 and 3, Brora 1).

b) Population size variation (mean  $\pm$  S.E.) along the two transects of the Scottish Robertsonian system, based on all successful trapping visits to farms.

**Reproductive conditions assessed on live individuals in the field**

Frequencies of pregnant and lactating females were not statistically different in the different zones ( $KW = 8.73$ ,  $p = 0.19$ ) and during the two trapping sessions ( $KW = 1.91$ ,  $p = 0.17$ ). The mean frequency was 13.0%. However, population size and frequency of pregnant and lactating females were significantly correlated (Spearman rank correlation  $n = 33$ ,  $r_s = 0.67$ ,  $p < 0.001$ ). The fewest pregnant and lactating females were found in the 32 zone (3%) where there was the lowest density of mice (3–10 mice/100 trap nights).



**Fig. 3.** Examples of weight structures observed in different mouse populations. (a) The “adult dominated” distribution observed in the 36 S chromosomal zone during both trapping sessions. (b) The “all age classes” distribution of weights frequencies observed in the 40 S chromosomal zone during the second trapping session.

The frequency of males with descended testes was significantly lower during the second session (18% of males) than the first (72% of males;  $KW = 7.84$ ,  $p = 0.005$ ), indicating a greater sexual activity in the spring. There were no significant differences between chromosomal zones but the 34 W and 32 zones tended to have the lowest frequencies of such males.

### Reproductive conditions as assessed on post-mortem specimens after 3 months in the laboratory

Males of the 40 W, 40 S, 36 W, 36 S, and 32 chromosomal zones were compared for their testis and seminal vesicle size. Mice collected during session 1 were sacrificed in July 1992, those collected during session 2 in December 1992, we thus assumed that they were all adult when these organs were weighted, given that they were all at least 3 months old.

At the time the mice were sacrificed, there was no significant variation in body weight, neither between zones nor between time of sampling (Tab. 2).

**Table 2.** Body, testes and seminal vesicles weights (mean  $\pm$  SE) of mice from five different races of the Scottish hybrid zone sampled during the two trapping sessions.

Races	2 n = 40 W	2 n = 36 W	2 n = 32		2 n = 36 S		2 n = 40 S	
Trapping session	1	1	1	2	1	2	1	2
N	10	11	7	7	7	11	19 (*18)	14
Body weight at capture (g)	16.3 $\pm$ 0.9	16.5 $\pm$ 1.6	18.1 $\pm$ 1.5	15.1 $\pm$ 0.9	17.6 $\pm$ 0.6	16.9 $\pm$ 1.2	16.9 $\pm$ 0.7	14.9 $\pm$ 0.8
Body weight after 3 months in lab (g)	19.5 $\pm$ 0.6	17.4 $\pm$ 0.5	20.9 $\pm$ 1.3	20.2 $\pm$ 0.7	20.6 $\pm$ 0.4	19.5 $\pm$ 0.5	20.0 $\pm$ 0.5	19.0 $\pm$ 0.7
Testes weight (mg)	163.7 $\pm$ 6.1	158.0 $\pm$ 5.0	161.1 $\pm$ 7.8	167.8 $\pm$ 10.3	159.8 $\pm$ 4.8	157.6 $\pm$ 2.7	*116.6 $\pm$ 4.5	138.2 $\pm$ 4.2
Seminal vesicles weight (mg)	143.8 $\pm$ 22.8	64.3 $\pm$ 5.8	87.3 $\pm$ 12.0	108.9 $\pm$ 12.7	101.2 $\pm$ 11.5	107.8 $\pm$ 13.9	58.1 $\pm$ 6.8	68.5 $\pm$ 8.6
Seminal vesicles/Body weight ( $\times 10^{-3}$ )	7.2 $\pm$ 1.1	3.8 $\pm$ 0.4	4.1 $\pm$ 0.5	5.3 $\pm$ 0.5	4.9 $\pm$ 0.6	5.5 $\pm$ 0.6	2.9 $\pm$ 0.3	3.5 $\pm$ 0.3

Body weight and seminal vesicle weight were found to correlate positively both for mice collected during the first and second sessions ( $r_s = 0.43$ ,  $p = 0.001$ ,  $n = 57$  and  $r_s = 0.72$ ,  $p = 0.0001$ ,  $n = 32$ , respectively). Therefore, it was considered appropriate to express seminal vesicle weights per unit body weight. These "relative seminal vesicle weights" differed significantly between chromosomal zones for both the first session (Tab. 2; Anova,  $F_{4,49} = 8.83$ ,  $p = 0.0001$ ) and the second (Tab. 2;  $F_{2,29} = 5.47$ ,  $p = 0.01$ ). Mice from the 40 S zone had the lowest relative seminal vesicle weight and those from the 40 W zone, the highest.

Testis weights were not correlated with body weights and so raw values were compared (Tab. 2). Mice differed significantly among the different chromosomal zones during both trapping sessions (session 1:  $F_{4,48} = 17.45$ ,  $p < 0.001$ ; session 2:  $F_{2,29} = 8.13$ ,  $p = 0.002$ ). Mice from the 40 S zone were characterised by the lowest testis weights for both sessions ( $p < 0.05$ ).



## Discussion

### Habitat and population characteristics

House mice appear not to occur or to be rare in the outdoor (not agricultural fields) of Caithness and Sutherland. One can propose that either environmental conditions are not favorable for the house mouse to establish populations, still the house mouse is known to occur in various conditions when on islands (BERRY and BRONSON 1992), or the presence of competitors such as *Apodemus sylvaticus* would limit house mouse to commensal habitats (BERRY 1986; NAVAJAS Y NAVARRO et al. 1989). In the latter case, considering the geographical features of the area and the distribution of commensal habitats in Caithness and Sutherland, the chromosomal zones appear to be separated from each other by habitat unsuitable to mice, with the exception of the 34 W and 34 S and 36 S zones. Passive transport might represent the only means by which mice could move between most of the chromosomal zones.

Commensal habitats are considered to favour high densities of mice and to allow continuous reproduction (BRONSON 1979). Moreover, human habitat is thought to induce spatial substructure in mouse populations such that they would function more or less like metapopulations (BAKER 1990). Our results show that even though all mice studied were from commensal habitats, density and fertility could be variable. Low fertility was found where densities were low (the 32 zone). This result is surprising since one would expect that social influence would reduce the numbers of pregnant females in high density better than in low density populations (BRONSON 1989). As far as the populations studied here are concerned, density appears not to be high enough to provoke reproduction reduction. Lower fertility in the 32 zone may be related to unfavourable environmental conditions, or to genetic peculiarities of these mice.

Considering the variation in population structure across the hybrid zone there appears to be the following pattern (refer to Fig. 1). The 32 zone occupies a small area and consists of several small farms. The mice occur at low density and were the least fertile of the animals examined (in terms of number of pregnant and lactating females). The 34 and 36 zones occupy larger areas and consist of larger farms than in the 32 zone and the mice occur at high densities. Large farms and very high densities also occur in the 40 zones, but the 40 W zone, at least, is very restricted in area. The particularly low density of mice in farms from the 32 zone was confirmed during both trapping sessions in the present study and during other field trips by JBS (pers. obs.: 1987 and 1989) and CHRISTIANNE PALMER (pers. comm.: 1994).

### Features of farming in Caithness and Sutherland

Three characteristics are important to consider in relation to the dynamics of the Scottish Robertsonian system: the evolution of agricultural practices, human trade between chromosomal zones and the effects of poisoning.

In the agricultural triangle of NE Caithness (32, 34 W, 34 S chromosomal zones), traditional stacks for the long-term storage of unthreshed oats, used to be very common. These stacks provided food and shelter for mice. The replacement of threshing by combine harvesting over the last half-century has probably involved a dramatic change in mouse populations (BERRY 1981). The use of stacks certainly maintained very high density populations of mice in this area, with very few extinction events since poisons were not used in the stacks.

These days there are almost no traditional stacks. In 1992 we only observed them in two very localised areas of Caithness: in the village of Thrumster (36 S zone), and at one farm in John o'Groats. In 1989 there was also a stack in John o'Groats; trapping studies

have confirmed the extremely high density of mice that occur in such structures (GG and JBS pers. obs.)

At the time when stacks were commonly used in Caithness, mice might have been considerably more abundant in the 32, 34S and 34W zones than they are nowadays. In other parts of the studied area, agricultural practices probably have not changed so dramatically, because stacks were not used and farming consists mainly of stock breeding.

Another aspect of farms of considerable importance to our understanding of the Scottish hybrid zone is the degree of human contact between the different areas. Discussion with farmers from the different chromosomal zones provided us with interesting information regarding possible passive transport of the house mouse in this region. Within the 32, 34, and 36S zones there seems to be extensive movements of materials directly among farms or via cooperatives based in Wick. Farmers in the vicinity of John o'Groats also exchange agricultural goods with farmers in Orkney (archipelago north of Caithness). So, passive transport of mice could occur between these zones.

However, the farmers in the 32, 34 and 36S zones have few, if any, interactions with the 36W, 40W, and 40S farmers. In the 40S zone, farmers exchange materials among themselves and with farmers further south.

A final observation on farming practice relates to the effects of poisoning on populations of mice. Rodenticide is not commonly used in the area, but when applied can dramatically reduce mouse populations. For example, the farm at Crakaig had a very large population in March 1992 but no animals were caught in September 1992, apparently as a result of poisoning.

However, the farm had a substantial number of mice again in autumn 1994 (C.P. pers. obs.). Such "boom-bust" population changes, whether the result of poison or other factors, may have profound impact on the population genetics of the house mouse. If the mice actually go extinct during the poisoning phase then recolonisation of the farm involves migration of mice from elsewhere, causing gene flow and (in the context of the Scottish hybrid zone) chromosomal flow. If the mice do not go extinct, then the poisoning phase may represent a population bottleneck causing enhanced genetic drift and decreased genetic heterozygosity. These constitute important factors which could influence the rates of fixation of Robertsonian fusions (MICHALAKIS and OLIVIERI 1993).

### **Difference in testis weight between 40S and other mice**

The specimens that were maintained in captivity for three months were very informative. Although individuals from the different chromosomal zones did not differ in body weight, the 40S males had smaller testes than mice from the other chromosomal zones. Testis weights have been examined for a second chromosomal hybrid zone in the house mouse. In Upper Valtellina (northern Italy), HAUFFE (1993) found that standard mice had significantly larger testes than Robertsonian mice, contrary to our finding that certain standard race mice (40S) had small testes. Given this discrepancy and the difference in testis weights between the 40S (small testes) and 40W (large testes) mice in Scotland, there is clearly no consistent relationship between testis weight and karyotype.

Testis size may reflect the mating system of the individuals examined. Relatively large testes would be expected in species or populations where there is substantial sperm competition, i.e. a promiscuous mating system (KENAGY and TROMBULAK 1986). In shrews (*Sorex*), there is evidence that sperm competition is more likely when individuals are at high density (STOCKLEY and SEARLE, in prep.). Thus, on the basis of present population sizes, we may have expected 40S mice to have testis as large as 40W mice do, which is not the case. Investigations on inbred strains of the house mouse have shown considerable variation in testis size (HAYWARD and SHIRE 1974), and that at the different stages of the ontogenesis and growth of a mouse, testis size is under the control of the X and Y chromosomes as well as

autosomal genes (HUNT and MITTWOCH 1987; CHUBB 1992). Thus small testes in mice from the 40 S zone may reflect genetic variability between populations of mice.

### Evolution of the Scottish hybrid zone

It is difficult to make any sensible deductions about the origin of the 32-chromosome race in Caithness from our ecological studies. It could have arisen at any stage during the 2,000 years the house mouse are known to have existed in Britain (BROTHWELL 1981; NACHMANN et al. 1994). It is not clear, for instance, whether the race arose when the density of mice was low or high, although further archaeological studies and genetical analysis may give some insight into this point.

One interesting feature of the hybrid zone between the 32-chromosome John o'Groats race and 40-chromosome standard race is that it has a staggered structure. Thus, instead of the 40-chromosome race directly abutting the 32-chromosome race, there is an intermediate 36-chromosome form (and mice with 34 chromosomes are found at the contact of the 32- and 36-chromosome races). This staggered structure could have arisen at the time of formation of the hybrid zone or it could have been a more recent event (SEARLE 1991; SEARLE et al. 1993). While our ecological study does not help us distinguish between the various models to explain the origin of the staggered hybrid zone, it shows that human behaviour could be very important to take into account in order to understand population features of the commensal house mouse.

Changes in population density over the last 50 years may have influenced the degree of staggering within the hybrid zone. To illustrate this we present one possible scenario. We propose that the agricultural triangle in northeastern Caithness, presently incorporating both the 32 and 34 chromosomal zones, may have formerly been occupied almost exclusively by 32-chromosome mice, at high density because of the presence of many oat stacks. This 32 zone could have been in equilibrium with neighbouring 34 zones, with a balance of dispersal in and out of the agricultural triangle. However, with the disappearance of the oat stacks and decrease in mouse density within the agricultural triangle, there may, in recent times, have been a greater tendency for mice to migrate into the triangle than out. In this way, the acrocentrics 6, 11, 13 and 14 (found in the 34 zones) may have penetrated the 32 zone (characterised by metacentrics 6.13 and 11.14), such that the 34 zones moved into the agricultural triangle. A 34 zone represents polymorphism, such that chromosomes 6, 11, 13, 14, 6.13 and 11.14 are all found in the same area. Thus the separation (or "stagger") of the John o'Groats and standard races would have been enhanced.

Clearly, on this scenario, the acrocentrics 6, 11, 13 and 14 may be continuing to spread at the expense of metacentrics 6.13 and 11.14. If so, and unless behavioural traits inhibit the spread of "foreign" mice into the 32 zone GANEM and SEARLE in press., ultimately the 32-chromosome race may go extinct such that the agricultural triangle will become occupied by the 36-chromosome race. Whether or not the hybrid zone has been evolving in this way, the John o'Groats race does appear to be endangered. It occurs in a very limited area at low density and may be susceptible to extinction by disease or further adverse changes in agricultural practice.

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## Zusammenfassung

### *Ein ökologischer Vergleich zwischen Standard- und chromosomal abweichenden Hausmäusen in Nordschottland*

Im Westen Europas kommen Populationen der Hausmaus vor, die als Folge Robertson'scher Fusionen vom Standard-Chromosomensatz ( $2n = 40$ ) abweichen. Über die Ökologie solcher Robertson'scher Hausmauspopulationen ist sehr wenig bekannt. Die vorliegende Arbeit behandelt ein karyotypisch heterogenes Gebiet im Nordosten Schottlands. Wir unterscheiden sieben „chromosomale Zonen“ entlang zweier Nord-Süd- bzw. Ost-West-Transsekte ( $2n = 32$  im äußersten Nordosten,  $2n = 34$  S(üden),  $2n = 34$  W(esten),  $2n = 36$  S,  $2n = 36$  W,  $2n = 40$  S,  $2n = 40$  W). Die verschiedenen chromosomalen Zonen werden bezüglich ihrer Habitat- und Populationseigenschaften beschrieben und verglichen. Die chromosomale Rasse  $2n = 32$  ist durch die niedrigste Dichte sowie die geringste Häufigkeit von trächtigen und säugenden Weibchen charakterisiert. Die höchsten Dichten wurden in beiden  $2n = 40$  Zonen gefunden. Intermediäre chromosomale Zonen scheinen durch Habitat voneinander getrennt zu sein, in dem die Hausmaus nicht vorkommt. Folglich wäre passiver Transport das einzige Mittel, durch das sich Mäuse zwischen den Zonen bewegen können. In den Zonen 32, 34 und 36 S finden landwirtschaftliche Transporte statt, während die Bauern dieser Gebiete, wenn überhaupt, nur wenig Kontakt zu Bauern der anderen Zonen haben. Dieses Muster landwirtschaftlicher Beziehung sollte chromosomalen Fluß zwischen den Zonen 32, 34 und 36 S erleichtern und diese von den anderen drei Zonen isolieren. Durch chromosomalen Fluß zwischen der Zone 32 und den angrenzenden Gebieten könnte die durch niedrige Dichte und geringe Fruchtbarkeit gekennzeichnete  $2n = 32$ -Rasse vom Aussterben bedroht werden.

## References

- AUFFRAY, J.-C.; BELKHIR, K.; CASSAING, J.; BRITTON-DAVIDIAN, J.; CROSET, H. (1990 a): Outdoor occurrence in Robertsonian and standard populations of the house mouse. *Vie et Milieu* **40**, 111–118.
- AUFFRAY, J.-C.; VANLERBERGHE, F.; BRITTON-DAVIDIAN, J. (1990 b): The house mouse progression in Eurasia: a paleontological and archaeozoological approach. *Biol. J. Lin. Soc.* **41**, 13–25.
- BAKER, A. E. M. (1990): Does group selection occur in commensal house mice (*Mus domesticus*)? In: Living in a patchy environment. Ed. by B. SHORROCKS and I. R. SWINGLAND Oxford: Oxford Science Publ. Pp. 197–218.
- BAUCHAU, V. (1990): Phylogenetic analysis of the distribution of chromosomal races of *Mus musculus domesticus* Rütty in Europe. *Biol. J. Linn. Soc.* **41**, 171–192.
- BERRY, R. J. (1981): Town mouse, country mouse: adaptation and adaptability in *Mus domesticus* (*M. musculus domesticus*). *Mammal Rev.* **11**, 91–136.
- BERRY, R. J. (1986): Genetical processes in wild mouse populations. Past myth and present knowledge in current Topics in Microbiology and Immunology, Vol. **127**, 86–94.
- BERRY, R. J.; BERRY, A. J.; ANDERSON, T. J. C.; SCRIVEN, P. (1992): The house mice of Faray, Orkney. *J. Zool. London* **228**, 233–246.
- BERRY, R. J.; BRONSON, F. H. (1992): Life history and bioeconomy of the house mouse. *Biol. Rev.* **67**, 519–550.
- BRONSON, F. H. (1979): The reproductive ecology of the house mouse. *Quart. rev. Biol.* **54**, 265–299.
- BRONSON, F. H. (1989): Mammalian reproductive biology. Chicago, London: Univ. of Chicago Press.
- BROTHWELL, D. (1981): The Pleistocene and Holocene archaeology of the house mouse and related species. *Symp. Zool. Soc. London* **47**, 1–13.
- CHUBB, C. (1992): Genes regulating testis size. *Biol. Reprod.* **47**, 29–36.
- GANEM, G. (1991): Commensalisme, fonction cortisosurrénalienne et évolution chromosomique chez la souris domestique. Thèse de Doctorat, Université Montpellier II.
- GANEM, G. (1993): Ecological characteristics of the house mouse Robertsonian populations. Is their habitat relevant to their evolution? *Mammalia* **57**, 349–357.
- GANEM, G.; SEARLE, J. B. (in press): Behavioural discrimination among chromosomal races of the house mouse (*Mus musculus domesticus*) in *J. Evol. Biol.*
- HAUFFE, H. C. (1993): Robertsonian fusions and speciation in a house mouse hybrid zone. DPh thesis, University of Oxford.
- HAYWARD, P.; SHIRE, J. G. M. (1974): Y chromosome effect on adult testis size. *Nature* **250**, 499–450.

- HUNT, S. E.; MITTWOCH, U. (1987): Y-chromosomal and other factors in the development of testis size in mice. *Genet Res. Camb.* **50**, 205–211.
- KENAGY, G. J.; TROMBULAK, S. C. (1986): Size and function of mammalian testes in relation to body size. *J. Mammalogy* **67**, 1–22.
- MICHALAKIS, Y.; OLIVIERI, I. (1993): The influence of local extinctions on the probability and time to fixation of chromosomal rearrangements. *J. Evol. Biol.* **6**, 153–171.
- NACHMAN, M. W.; BOYER, S. N.; SEARLE, J. B.; AQUADRO, C. F. (1994): Mitochondrial DNA variation and the evolution of Robertsonian chromosomal races of house mice, *Mus domesticus*. *Genetics* **136**, 1105–1120.
- NAVAS Y NAVARRO, M.; CASSAING, J.; CROSET, H. (1989): Démographie et dispersion d'une population sauvage insulaire de *Mus musculus domesticus*: comparaison avec une population continentale. *Z. Säugetierkunde* **54**, 286–295.
- SAÏD, K.; BRITTON-DAVIDIAN, J. (1991): Genetic differentiation and habitat partition of Robertsonian house mouse populations (*Mus musculus domesticus*) of Tunisia. *J. Evol. Biol.* **4**, 409–427.
- SCRIVEN, P. N.; BROOKER, P. C. (1990): Caithness revisited: Robertsonian chromosome polymorphism in Caithness house mice. *Heredity* **64**, 25–27.
- SEARLE, J. B. (1991): A hybrid zone comprising staggered chromosomal clines in the house mouse (*Mus musculus domesticus*). *Proc. R. Soc. London B* **246**, 47–52.
- SEARLE, J. B.; NARAIN NAVARRO, Y.; GANEM, G. (1993): Further studies of a staggered hybrid zone in *Mus musculus domesticus* (the house mouse). *Heredity* **71**, 523–531.

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